



Future climate change likely to reduce the Australian plague locust (*Chortoicetes terminifera*) seasonal outbreaks

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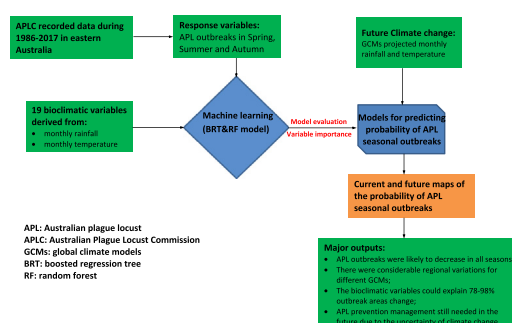
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HIGHLIGHTS

- A 32-year locust survey database was used to study the occurrence of locust outbreak.
- Both RF and BRT models had good performance in predicting APL spring outbreaks.
- Bio15 and Bio11 had a high explanatory power to APL spring outbreaks.
- APL outbreak areas were likely to decrease in all seasons under future climate change.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate is a major limiting factor for insect distributions and it is expected that a changing climate will likely alter spatial patterns of pest outbreaks. The Australian plague locust (APL) *Chortoicetes terminifera*, is the most economically important locust species in Australia. Invasions cause large scale economic damage to agricultural crops and pastures. Understanding the regional-scale and long-term dynamics is a prerequisite to develop effective control and preventive management strategies. In this study, we used a 32-year locust survey database to uncover the relationship between historical bioclimatic variables and spatial seasonal outbreaks by developing two machine learning species distribution models (SDMs), random forest and boosted regression trees. The explanatory variables were ranked by contribution to the generated models. The bio-climate models were then projected into a future climate change scenario (RCP8.5) using downscaled 34 global climate models (GCMs) to assess how climate change may alter APL seasonal distribution patterns in eastern Australia. Our results show that the model for the distribution of spring outbreaks performed better than those for summer and autumn, based on statistical evaluation criteria. The spatial models of seasonal outbreaks indicate that the areas subject to APL outbreaks were likely to decrease in all seasons. Multi-GCM ensemble means show the largest decrease in area was for spring outbreaks, reduced by 93–94% by 2071–2090, while the area of summer outbreaks decreased by 78–90%, and 67–74% for autumn outbreaks. The bioclimatic variables could explain 78–98% outbreak areas change. This study represents an important step toward the assessment of the effects

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of the changing climate on locust outbreaks and can help inform future priorities for regional mitigation efforts in the context of global climate change in eastern Australia.

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1. Introduction

Locusts have historically been and remain significant insect pests because of their destructive impacts on agricultural production in many countries (Chapuis et al., 2011; Meynard et al., 2017; Murray et al., 2013; Zhang et al., 2009). Species of the Acrididae known as locusts exhibit phase polyphenism, where individuals of the same genotype display different phenotypes that incorporate variations in morphology, behaviour, coloration and reproductive features (Pener and Simpson, 2009; Topaz et al., 2012). An individual can change from a solitary state to a gregarious one, which depends on local population density. For example, in sparse surroundings a gregarious locust transitions to the solitary state and vice versa in crowded environments. In the gregarious phase locusts produce large, high density migratory populations that can be sustained over multiple generations. The demographic consequences can result in widespread crop and pasture damage. This has been a global issue due to its devastating impacts on world's national agricultural products and livelihoods (<http://www.fao.org/food-chain-crisis/how-we-work/plant-protection/locusts/en/>).

Australian agriculture contributes significantly to the global food market, primarily through crop and livestock production (Cleugh et al., 2011; Qureshi et al., 2013). The endemic Australian plague locust (APL), *Chortoicetes terminifera*, has been the most economically important and widespread locust pest of agriculture in the temperate cropping lands of mainland Australia (Deveson, 2013; Hunter et al., 2001). APL outbreaks can affect not only the quantity or quality of these products, but also can indirectly affect food security, market development and international trade (Adriaansen et al., 2016). It is reported that estimated annual economic loss for the main crops due to APL can be up to \$28.4 million in Australia (Murray et al., 2013). Severe agricultural impacts can occur in autumn when winter grain crops are emerging or in spring when they reach reproductive stage (Murray et al., 2013).

Researchers have long associated APL outbreaks with rainfall because it regulates plant productivity in the semi-arid rangeland habitats. Previous studies used simulation models of locust phenology and water-balance to reconstruct the development of historical APL plagues (Wright, 1987). Therefore, the relationship between rainfall and habitat productivity became the basis for operational surveillance and short-term forecasting. From the 1980s, satellite remote sensing imagery became a focus of research on monitoring locust habitat with green vegetation to indicate likely population increase (Bryceson, 1990; Deveson, 2013). However, there are numerous other environmental constraints on population increase, including behavioural, habitat and trophic interactions as well as human land use. There is worldwide evidence that environmental changes resulting from agricultural practices have altered the outbreak frequencies of many locust and grasshopper species (Benfeki et al., 2002; Cease et al., 2012). The complexities of these total environment ecological interactions make prediction of APL outbreaks in future decades problematic.

Climate changes, such as increases in temperature and changes of rainfall patterns, have become dominant drivers of global biodiversity change (Warren et al., 2013). There is general agreement that climate change will significantly affect the future distribution of mammals, birds and insects, as well as crop plants (Ramirez-Cabral et al., 2017; Wang et al., 2018a; Warren et al., 2013; Zhao et al., 2018). Machine learning species distribution models (SDMs), which quantify the relationship between species and their environment based on occurrence data, are frequently used to define the environmental characteristics of current species distributions. Calibrated models of species

distributions are projected into future climate space to evaluate the likely effects of climate change on the distribution boundary and suitable environmental conditions. These models can predict the expected effects of changing climate on the probability of a species' occurrence. For example, Macfadyen et al. (2018) predicted that there would be a substantial decrease in the areas suitable for four widespread pests of brassica crops over the continent of Australia by 2090, mainly due to climate warming. The climate suitability for several insect pests tends to shrink and shift from north to south under future climate conditions in Australia. Ramirez-Cabral et al. (2018) concluded that the distribution area of soybean rust and beet armyworm is likely to be reduced and shift away from the equator toward high-latitude areas on the global scale due to future heat stress and drought.

SDMs are reliable for modelling the spatial distribution of invasive species (Lamsal et al., 2018; Macfadyen et al., 2018; Shrestha et al., 2018; Thapa et al., 2018). They are able to identify the relative importance of climate variables that are correlated with broad distribution patterns. Recently, Meynard et al. (2017) used historical data on the distribution of solitary locusts from the two subspecies of *Schistocerca* that occur in Africa to build SDMs and then applied those models to predict changes in the distribution limits of both under several models of future climate change. Although APL researchers also attempted to identify key features from relevant environmental conditions to match historical records of locust distribution through various statistical methods, no studies have applied machine learning approaches on the broad region of APL outbreaks to identify what environmental predictors are responsible for determining their occurrence and extend the time dimension of climate forecasts decades in advance to project likely impacts of future climate on APL suitability.

In this study we applied two widely used species distribution models to a long-term georeferenced data set of locust abundance collected by the Australian Plague Locust Commission (APLC), to explore the relationship between the seasonal outbreaks of APL and historical bioclimatic variables. We assessed changes in the spatial distribution of APL seasonal outbreaks in 2031–2050, 2051–2070 and 2071–2090 periods relative to 1986–2017 in eastern Australia. Local-scale climate scenarios were based on the downscaled data from 34 Global Climate Models (GCMs) from the Coupled Model Intercomparison Project Phase 5 (CMIP5) multi-model ensemble (Taylor et al., 2012) and Representative Concentration Pathways (RCP) 8.5 (Moss et al., 2010). The resulting models were used to predict the long-term distribution of the probability of seasonal outbreaks under future climate scenarios. The objectives of this study were to (1) identify the dominant climate predictors of the distribution of Australian plague locust outbreaks at a fine spatial scale; (2) predict the distribution of the probability of APL outbreaks under future climate change scenarios; (3) quantify the influence of climate change on the future spatial distribution of APL outbreaks.

2. Materials and methods

2.1. The study area and locust data

The study region covers inland areas across four states (Fig. S1), Queensland (QLD), New South Wales (NSW), Victoria (VIC) and South Australia (SA), where Australian plague locust populations have been monitored and recorded by APLC and state agriculture agencies. Across the study area, annual rainfall increases from west to east (150–650 mm) and annual mean temperature increases from south to north (21–33 °C). The rainfall pattern presents a strongly seasonal character with a uniform or winter maximum in the south (>30° S) and a

summer regime in the north. Large areas of western QLD, western NSW and northern SA are climatically arid (<250 mm) with very high rainfall variability. Locust habitats are mostly on inland plains with open tussock grassland and grassy open woodland vegetation, occupying ~1 million km⁻² (Fig. S1).

APL is migratory and widely distributed across the Australian mainland. It produces 2–4 continuous generations, depending on latitude and seasonal rainfall. These often correspond to the southern hemisphere spring, summer and autumn, although generation overlap and mixing is common. There is spatial correspondence between consecutive generations, but migrations can displace populations between regions. For example, the majority of spring outbreaks result from adult oviposition during autumn, many of which may have been immigrants. During winter the bulk of the population exists as dormant eggs, particularly in the southern part of the range. Outbreak development and persistence is also reinforced by migrations between habitats across summer and winter dominant rainfall regions (Deveson and Walker, 2005).

The APLC has conducted regular monitoring surveys and locust control actions since 1977. Records have included field-collected GPS coordinates since 1992 and for 1986–1992 were re-calculated from map coordinates. Survey procedures were designed to detect high density populations and the records include information on abundance of all identified life stages of several species from 250 m near-road transects. Statistical analysis of APL population dynamics has been limited by missing data for regular time intervals (Veran et al., 2015). Most data used in this study were extracted from the APLC database. From ~360,000 total records, there were 117,012 georeferenced recordings of APL over a period of 32 years from 1986 to 2017. In addition, 15,935 records of APL were collected by state government agencies.

For this study, we focused on the densities of locust nymphs from 132,947 APL records, because adults can migrate long distances (hundreds of kilometres) if weather conditions are suitable (Veran et al., 2015). Outbreaks are characterised by aggregated populations of nymphs, known as bands, up to 5000 m⁻², with gregarious phase behaviour. These represent agriculturally relevant population events. Recorded nymph densities >30 m⁻² were taken as a threshold to indicate actual or potential gregarious outbreaks, their location representing successful breeding and suitable habitat. At low densities, there is a lower probability of detection and records are more liable to identification error, so records are not a measure of nymph presence/absence.

To reduce the spatial and temporal biases in the samples, we divided the survey area into a regular grid with a cell size of 0.25 × 0.25°. This resolution covered the range of cumulative displacement of nymphs without excessively reducing within-cell data availability (Deveson, 2013; Veran et al., 2015). Taking all subset points lying within each grid cell, any occurrence of nymph density ≥30 m⁻² was used to indicate outbreaks have occurred in that cell (denoted as **1**). If only lower density nymphs (<30 m⁻²) or no nymphs have ever been recorded in a grid cell, it was coded as no outbreak (denoted as **0**). We calculated the number of grid cells with outbreaks (**1**) for each month during 1986–2017 to show the frequency at that timescale. Table S1 shows peaks in outbreak cells during September–November, January and March, which correspond broadly to the three seasonal generation times for nymph distributions.

All cells were therefore divided into three seasons (spring: Sep–Nov, summer: Dec–Feb, autumn: Mar–May) and split by outbreak occurrence (**1**) or (**0**). The winter season is absent from the analysis because the majority of the population is in the egg stage during winter and surveys are rarely carried out. The geographical distribution of outbreaks for each season through the time series is shown in Fig. S2. Spring outbreaks occur uniformly across the southern parts of the study area (i.e. NSW, southern SA and VIC). By contrast, summer and autumn outbreaks have a wider distribution throughout the study area, with numerous gaps where high density nymphs have not been recorded.

2.2. Climate data and bioclimatic variables

The observed daily climate data for rainfall, maximum and minimum temperature for the historical period (1986–2017) in ~5000 sites across eastern Australia were downloaded from SILO (Scientific Information for Land Owners) operated by Queensland Government's Open Data program (<https://legacy.longpaddock.qld.gov.au/silo/>) (Jeffrey et al., 2001).

For future climate scenarios, a total of 34 Global Climate Models (GCMs) (Table S2) were used. We considered three future time periods (e.g. 2031–2050, 2051–2070 and 2071–2090) to compare climate change with the historical period 1986–2017. The employment of numerous GCMs captures the variability in future climate projections arising from uncertainties in model structure and parameterization, and is a standard approach in climate impact studies (<http://www.ipcc.ch/report/ar5/>). We focused on a high emission scenario of Representative Concentration Pathway (RCP) experiments RCP8.5, which represents a future of no climate mitigation policies and would result in a radiative forcing reaching almost 8.5 W m⁻² (~936 ppm CO₂ concentration) by 2100 (Van Vuuren et al., 2011). We chose RCP8.5 because it is a worst climate change scenario and others show a more optimistic condition. In addition, more GCMs outputs are available for the RCP8.5 scenario.

Monthly gridded climate data from 34 GCMs included in the Coupled Model Intercomparison Project Phase 5 (CMIP5, <http://cmip-pcmdi.llnl.gov/cmip5/index.html>) were downsampled to daily temperature and rainfall at each site, following a statistical downscaling method developed by NSW Department of Primary Industries Wagga Wagga Agricultural Institute (Liu and Zuo, 2012). This statistical downscaling approach firstly employs an inverse distance-weighted (IDW) interpolation method, and then bias correction is applied by transferring the resulting monthly site data using functions obtained from analysing observed and GCM data for the historical training period. Daily climatic variables (e.g. maximum temperature, minimum temperature and rainfall) were then generated for each site from the spatially downsampled projections by using a modified version of the WGEN stochastic weather generator (Richardson and Wright, 1984). The method has been used in several recent climate change studies (Li et al., 2017; Liu et al., 2017; Wang et al., 2016; Wang et al., 2018a). Further details of the downscaling approach can be referred to Liu and Zuo (2012).

The downsampled daily rainfall, maximum and minimum temperature data were used to calculate future bioclimatic variables. As the distribution of APL outbreaks was gridded at 0.25°, the climate data for each cell was derived from the geographically closest site to each grid cell. 14 different bioclimatic variables (Table S3) for each season were chosen from 19 original bioclimatic variables (<http://www.worldclim.org/bioclim>) based the requirements of the APL lifecycle. We have concentrated only on bioclimatic variables because there are no equivalent datasets available on trophic or ecological interactions with other animal or plant species.

These bioclimatic variables depict yearly and seasonal tendency of rainfall and temperature and have been widely recognized as an adequate characterization of the species bioclimatic niches (Ye et al., 2018). The selected bioclimatic variables defined the baseline climate during the period 1986–2017. To model future distributions of seasonal outbreaks, we used average monthly rainfall and temperature in 2031–2050 (hereafter referred to as 2040s), 2051–2070 (2060s) and 2070–2090 (2080s) based on 34 GCMs in each grid cell of the study area to derive the corresponding 14 bioclimatic variables for each season. Only dynamic bioclimatic variables rather than biophysical, environmental or land cover variables were employed in our study as the focus was changing climatic suitability and long-term future data on environmental variables were unavailable (Porfiro et al., 2014).

2.3. Species distribution models (SDMs)

We selected two common classification algorithms used in machine learning to explore relationships between historical seasonal outbreak

occurrence and the 14 bioclimatic variables; random forest (RF) (Breiman, 2001) and boosted regression tree (BRT) (Elith et al., 2008). These two tree-based models were used because they are flexible and not computationally expensive and have been widely used in numerous ecological studies (Assis et al., 2018; Mędrzycki et al., 2017; Scherrer et al., 2017). They are also able to demonstrate the relative importance of each predictor variable. To date, there are no studies that have used BRT and RF models to explore the occurrence of APL seasonal outbreaks in eastern Australia. The R statistical packages *randomForest* (<https://cran.r-project.org/web/packages/randomForest/randomForest.pdf>) and *dismo* (<https://cran.r-project.org/web/packages/dismo/dismo.pdf>) were used to run RF and BRT, respectively.

2.4. Evaluation of model performance

We used the area under the curve (AUC) of the Receiver Operator Characteristic (ROC) plot and Cohen's Kappa statistic to evaluate model performance. These statistics have been widely applied as metrics of accuracy for SDMs (Thapa et al., 2018; Ye et al., 2018). The range of AUC value is 0–1 with values >0.8 considered as good model performance (Radinger et al., 2017). Kappa values also range from 0 to 1 and values >0.4 were considered moderate (Reis et al., 2018). All AUC and Kappa calculations were implemented with the *ROCR* package (<https://cran.r-project.org/web/packages/ROCR/ROCR.pdf>) for the R programming environment.

Each SDM was trained using data from a random selection of 75% of all grid cells for each season, with data for the remaining 25% of cells reserved to test model performance. To ensure a robust estimate of model performance, this procedure was repeated 100 times by applying a sampling with replacement method (Wang et al., 2018b). Then 100 random subsets of the data were obtained, each one with its own calibration and test dataset. Finally, 100 calibrated models and model evaluation criteria were returned for each season and per algorithm. To reduce the uncertainty of each SDM for future projections in the following analysis, we established an ensemble from 100 model outputs of each SDM by using a weighed mean approach that weights each model output according to predictive performance (Radinger et al., 2017; Shrestha et al., 2018).

2.5. Analysis of changes in areas of seasonal outbreaks

We mapped the probabilistic prediction for each GCM and seasonal SDM under each of the three (2040s, 2060s and 2080s) future climate scenarios. A probability threshold of 0.5 was used to distinguish outbreak and no outbreak in each pixel. Values ≥ 0.5 areas are plotted to indicate where habitat conditions remain suitable for locust outbreaks, while values < 0.5 represent low suitability of habitat for outbreaks. We counted the number of grid cells that are suitable for outbreaks (probability ≥ 0.5) for each GCM under future scenarios. Then the future range change was calculated from the number of pixels with outbreaks under future climate conditions relative to baseline. To analyse changes in seasonal outbreak areas as a consequence of predicted future changing climate, we used a stepwise regression model implemented in the *MASS* package (<https://cran.r-project.org/web/packages/MASS/MASS.pdf>) to select the most explanatory and most parsimonious bioclimatic variables according to the smallest Akaike Information Criterion (AIC).

3. Results

3.1. Model validation and bioclimatic variable contribution

Using the validation subsets, all models predicted the distribution of APL outbreaks in spring well based on AUC and Kappa metrics (Fig. 1). Overall, the BRT model performed slightly better than the RF model for spring outbreaks. The average AUC and Kappa value based on 100 runs for RF model was 0.93 and 0.73, respectively (Table S4). For the

spring BRT model, the average AUC was 0.94 and Kappa was 0.74 (Table S4). For summer and autumn outbreak models, the two algorithms presented similarly good performance according to the AUC criterion. The average AUC for both RF and BRT model was 0.80 in summer and 0.81 in autumn. However, the Kappa metric for the RF model had an average value of 0.42 in summer and 0.43 in autumn, a better performance than the BRT model with average Kappa of 0.31 in summer and 0.34 in autumn.

We estimated the importance values of each climatic variable for each season using both models. To obtain consistent values for each variable, we calculated the average importance using the 100 model runs during model training. RF and BRT showed different patterns of variable importance for individual seasons (Fig. 2). Specifically, the BRT indicated Bio11 (Mean Temperature of Coldest Quarter), Bio15 (Precipitation Seasonality), Bio4 (Temperature Seasonality), Bio1 (Annual Mean Temperature) and Bio9 (Mean Temperature of Driest Quarter) were the top five important predictors for spring seasons, with contribution rates of 39.8%, 22.3%, 4.2%, 4.1% and 3.6%, respectively. Bio14 (Precipitation of Driest Month) and Bio13 (Precipitation of Wettest Month) ranked as least important. By contrast, for the RF model, Bio15 (10.4%) became the most important predictors, followed by Bio11 (9.8%), Bio4 (8.8%), though the relative importance of each was close.

For summer seasons, the five most important predictors were Bio2 (Mean Diurnal Range, 11.2%), Bio9 (9.6%), Bio4 (9.1%), Bio1 (8.3%) and Bio14 (7.7%) in BRT model, which suggests temperature variables were more important than rainfall in the predictive models. The order of variable importance in the RF model was Bio2 (9.0%), Bio4 (8.2%), Bio17 (Precipitation of Driest Quarter, 7.9%), Bio1 (7.6%) and Bio14 (7.4%). Each predictor in both SDMs presented a comparable contribution. For autumn seasons, five variables showed a major role in predicting the distribution of outbreaks; Bio4 (22.4%), Bio17 (7.7%), Bio15 (7.5%), Bio14 (7.3%) and Bio9 (7.3%) in the BRT model. In the RF model the top five variables were Bio4 (10.9%), Bio17 (8.2%), Bio14

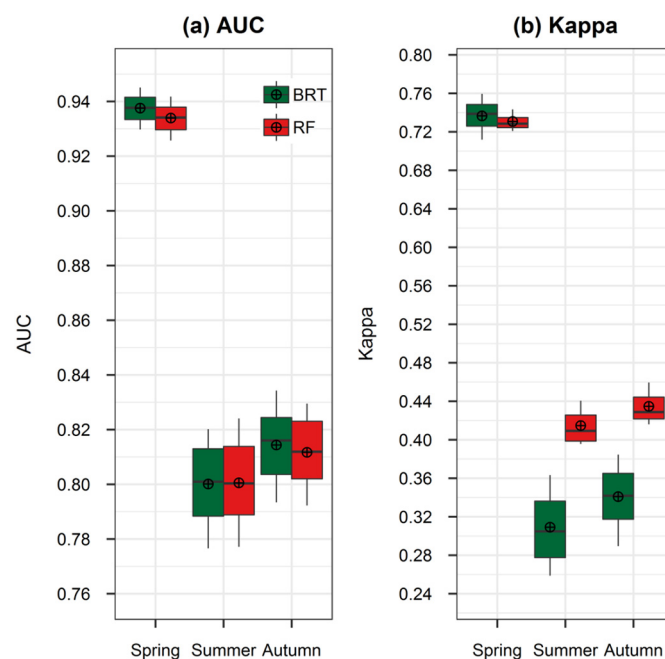


Fig. 1. Results of model evaluation criteria for prediction of Australian locust plague outbreaks in spring, summer and autumn using random forest (RF) model (red) and boosted regression tree (BRT) model (green) with 100 runs. Values presented are the area under the receiver operating characteristic (ROC) curve (AUC) and Cohen's Kappa statistic. The black lines within the box indicate the medians with 100 runs while crosshairs indicate means. Box boundaries indicate the 25th and 75th percentiles, whiskers below and above the box indicate the 10th and 90th percentiles. A good model will have an AUC >0.8 and a Kappa >0.4.

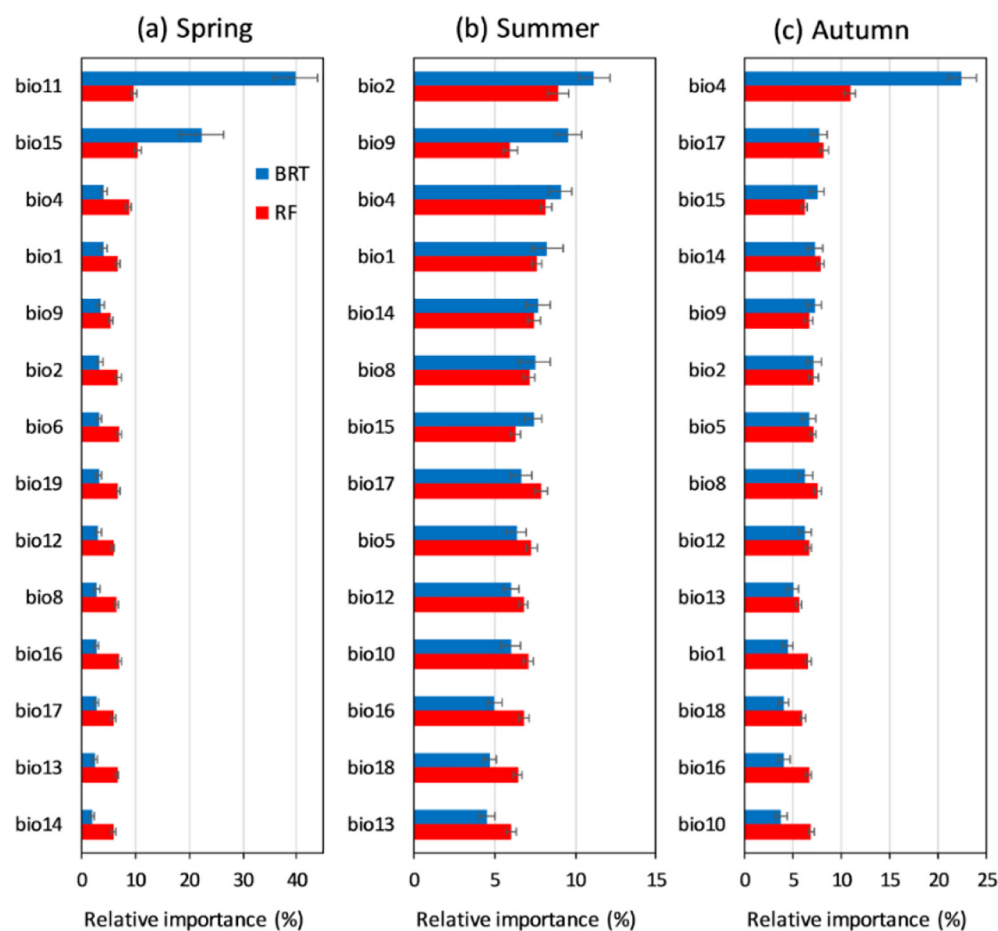


Fig. 2. The relative importance of each predictor variable used in random forest (RF) and boosted regression tree (BRT) models to predict the spatial distribution of Australian locust plague outbreaks in spring, summer and autumn. Values are mean \pm SDs based on 100 runs. Each variable was scaled to sum to 100%.

(7.9%), Bio8 (Mean Temperature of Wettest Quarter, 7.6%) and Bio2 (7.1%).

Based on the results of the relative contribution of each variable, we plotted the relationships between two dominant climate factors and the probability of APL seasonal outbreaks for the RF and BRT models (Fig. 3).

These figures help to illustrate how important variables interactively affect the spatial distribution of locust outbreak on a probability scale. Both machine learning techniques produced similar patterns of predictor interaction on the probability of outbreaks. For example, the suitable range of Bio11 and Bio 15 for spring outbreaks was less than

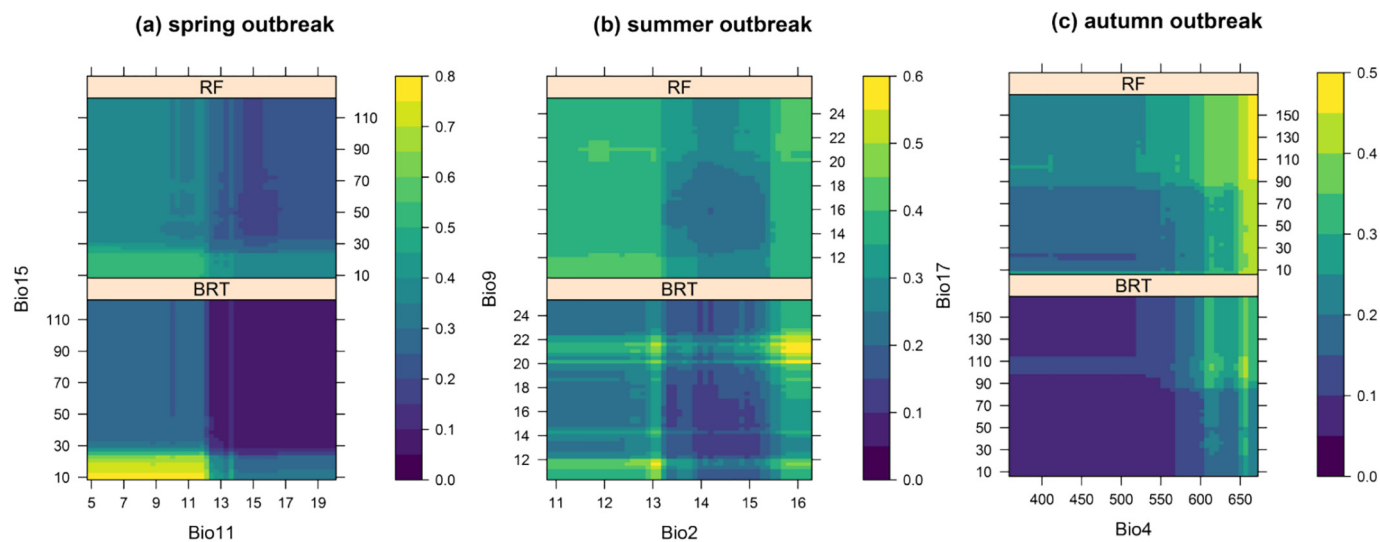


Fig. 3. Random forest (RF) and boosted regression tree (BRT) partial dependence of geographic distribution of APL seasonal outbreaks on two of the most important bioclimatic variables (see Fig. 2) plotted on the probability scale. Bio 15: Precipitation Seasonality, Bio11: Mean Temperature of Coldest Quarter, Bio9: Mean Temperature of Driest Quarter, Bio2: Mean Diurnal Range, Bio17: Precipitation of Driest Quarter, Bio 4: Temperature Seasonality.

approximately 13 °C and 30%, respectively (Fig. 3a). Summer APL outbreaks were mostly located in approximately 12.5–13.1 °C and 15.5–16.2 °C for Bio2 and 20–22 °C for Bio9 (Fig. 3b). Autumn APL outbreak events were more likely when Bio4 was >600% and Bio17 was >90 mm (Fig. 3c).

3.2. Future climate suitability projections

We utilized the derived SDMs to explore the influence of climate change on the future spatial distribution of APL outbreaks. The maps of the probability of APL seasonal outbreaks were classified into two classes: 0–0.5 with no outbreaks and 0.5–1.0 with outbreaks. For simplicity, the probability maps for the three seasons under the near future time period, viz. 2040s, projected by RF model are shown in Figs. 4, 5 & 6 (referred to Figs. S3–S8 for the other two future time periods in Supplementary information). The probability maps at different seasons under different future time periods projected by BRT are shown in Supplementary information (Figs. S9–S17).

Both SDMs suggested that by the 2040s there would be a decrease in the areas suitable for locust outbreaks in any season (Figs. 4–6 and Figs. S9, S12 and S15). However, there were regional differences for each GCM resulting from different climate projections. In general, areas in southern NSW, northern VIC and eastern SA were suitable in the 2040s, while areas in northern NSW and QLD suitable for spring outbreaks were reduced compared to baseline (Fig. 4 and Fig. S9). The trend to reduced areas of potential locust outbreaks continued in the 2060s and was most pronounced in the 2080s. This may be due to the expected very high rise in temperature and reduction of seasonal rainfall by the end of 21st century under RCP 8.5. The multiple GCM ensemble mean showed that the suitability of APL outbreaks projected by RF model in spring would decrease 46.8%, 75.8% and 93.7% in the 2040s, 2060s and 2080s, respectively (Fig. 7). The BRT model predicted a similar magnitude of decline in APL outbreak area for spring.

Compared with the future areas suitable for APL outbreaks in spring, the suitable areas in summer were more dispersed. The majority of GCMs projected that the most affected regions were in southern QLD,

eastern NSW and southern VIC by 2040s (Fig. 5 and Fig. S12). Over time, the APL outbreak areas continue to contract for most GCMs. By the 2080s, nearly 30 out of total 34 GCMs predicted that no summer outbreaks would occur in QLD (Fig. S6 and Fig. S14) and climatically suitable habitat for outbreaks will largely disappear. The multi-GCM ensemble mean showed the suitability of APL outbreaks projected by RF (BRT) model in summer would decrease 76.6% (73.1%), 83.4% (75.6%) and 90.1% (77.5%) in 2040s, 2060s and 2080s, respectively (Fig. 7).

Similar to summer outbreaks, APL outbreaks in autumn were dispersed (Fig. S2). By the 2040s, the majority of GCMs projected outbreak areas were mainly located at the border of QLD, NSW and SA (Fig. 6 and Fig. S15). Areas of APL outbreaks continued to contract by 2060s, apart from a few GCMs which showed a more neutral response (e.g. CaE, GF2 and FIO). By the 2080s, several GCMs (e.g. GE1, GE2, GF4 and MI3) projected climatic suitability for APL outbreaks would arise in new locations across four states, despite a continued decline in total suitable area. The multi-GCM ensemble mean showed the area suitable for autumn outbreaks projected by RF and BRT models would decrease 75.5% (67.5%), 81.8% (71.2%) and 74.4% (67.3%) in 2040s, 2060s and 2080s, respectively.

3.3. The contribution of climate change to predicted spatial changes in APL outbreak

To explore the contribution of each bioclimatic variable to the change in seasonal outbreak areas under projected future climates, we established a multiple linear regression model based on the results predicted by the 34 GCMs for three future time periods. Tables 1 and 2 show the relationships between the changes in climate variables and seasonal outbreaks areas for the RF and BRT model, respectively. The regression analysis quantifies the contribution of specific climate factors to the changes in area. We selected the most explanatory bioclimatic variables based on AIC for fitting each regression model. Similar climatic factors were chosen for both SDMs in the same season. In addition, the positive or negative significance of model coefficients was consistent

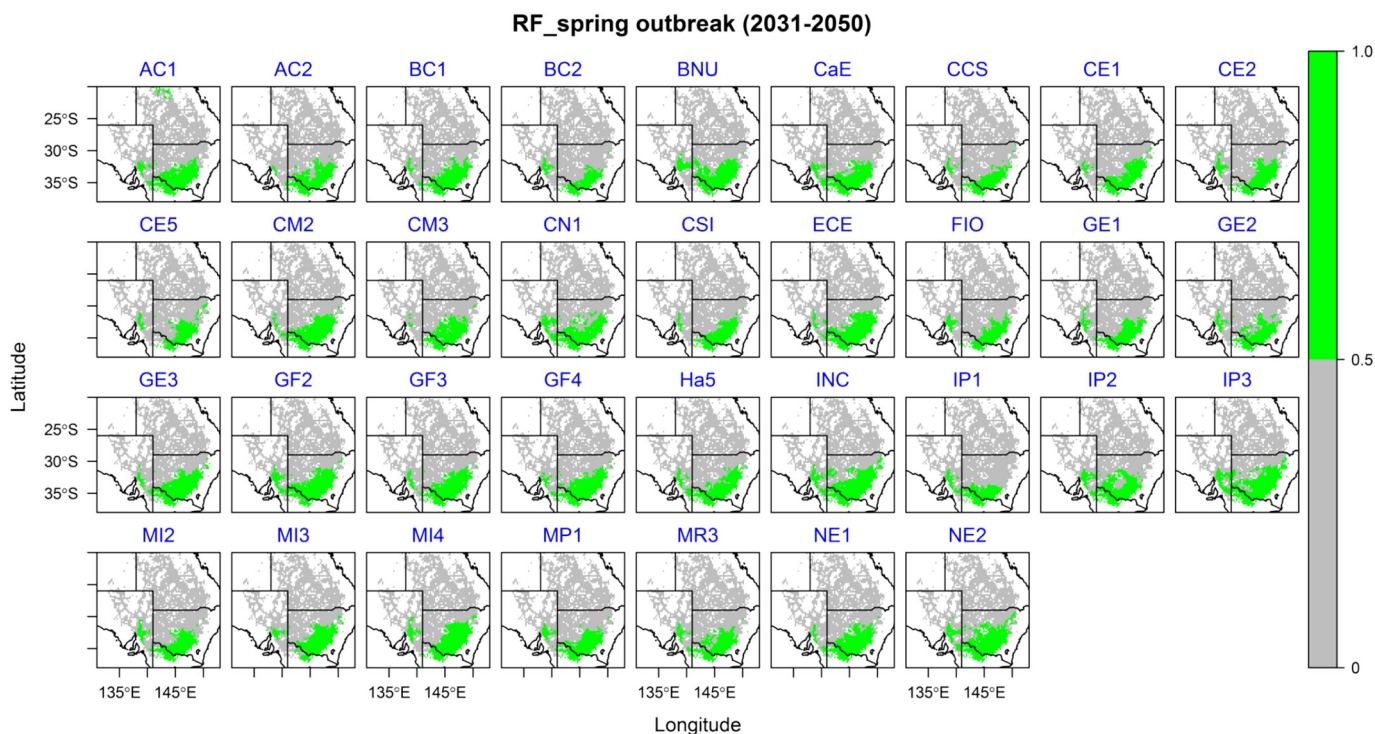


Fig. 4. The spatial distribution of the probability of Australian plague locust outbreaks in spring during 2031–2050 projected by random forest (RF) model based on climate projections from 34 GCMs under RCP8.5.

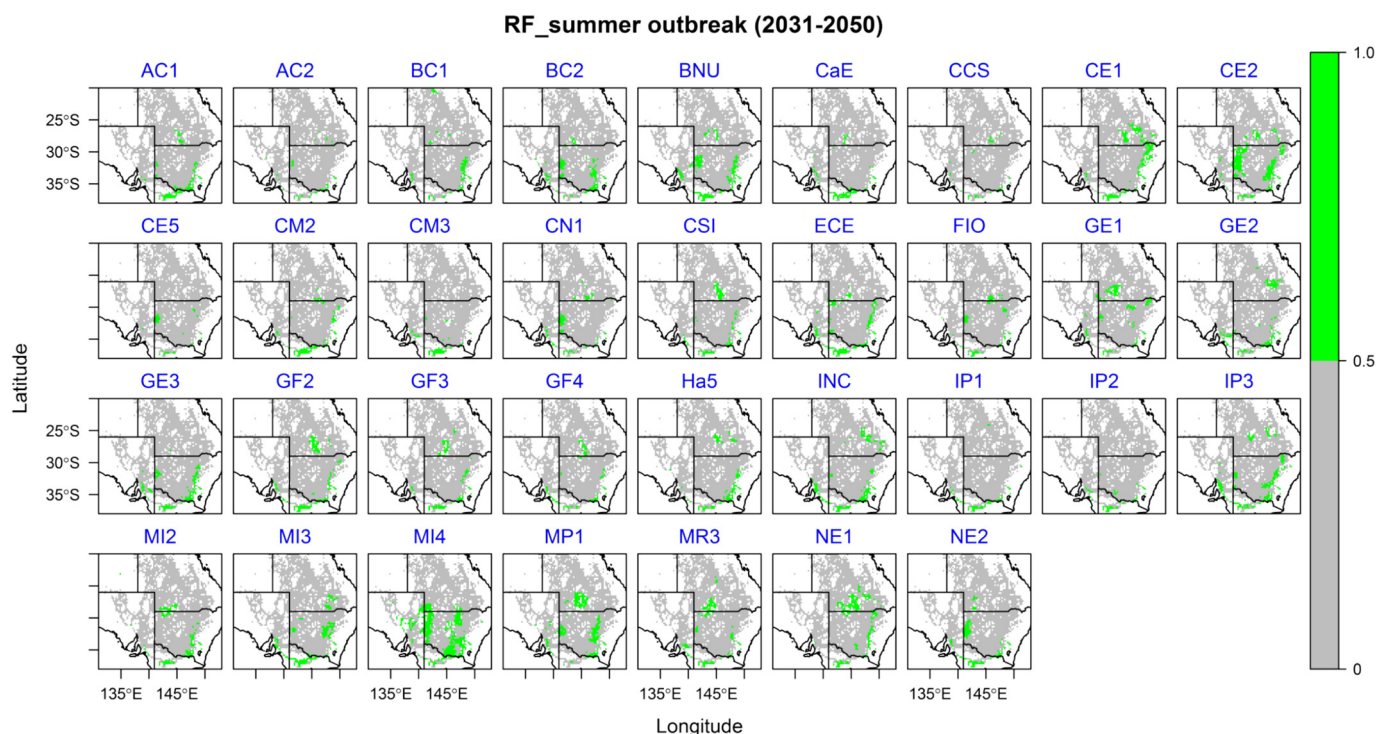


Fig. 5. The spatial distribution of the probability of Australian plague locust outbreaks in summer during 2031–2050 projected by random forest (RF) model based on climate projections from 34 GCMs under RCP8.5.

between the two SDMs for each season. For example, the temperature predictors (e.g. ΔBio10 and ΔBio11) were negatively correlated to change in outbreak area while rainfall indices (e.g. ΔBio14 and ΔBio16) were positively correlated. Both RF and BRF (all variables combined) accounted for 98% of spring area change, 91–93% in summer and 78–82% in autumn models (Tables 1 and 2).

4. Discussion

4.1. Model performance and bioclimatic variable importance

SDMs provide one method to characterise the distribution of locust outbreaks in eastern Australia. The 14 bioclimatic explanatory variables

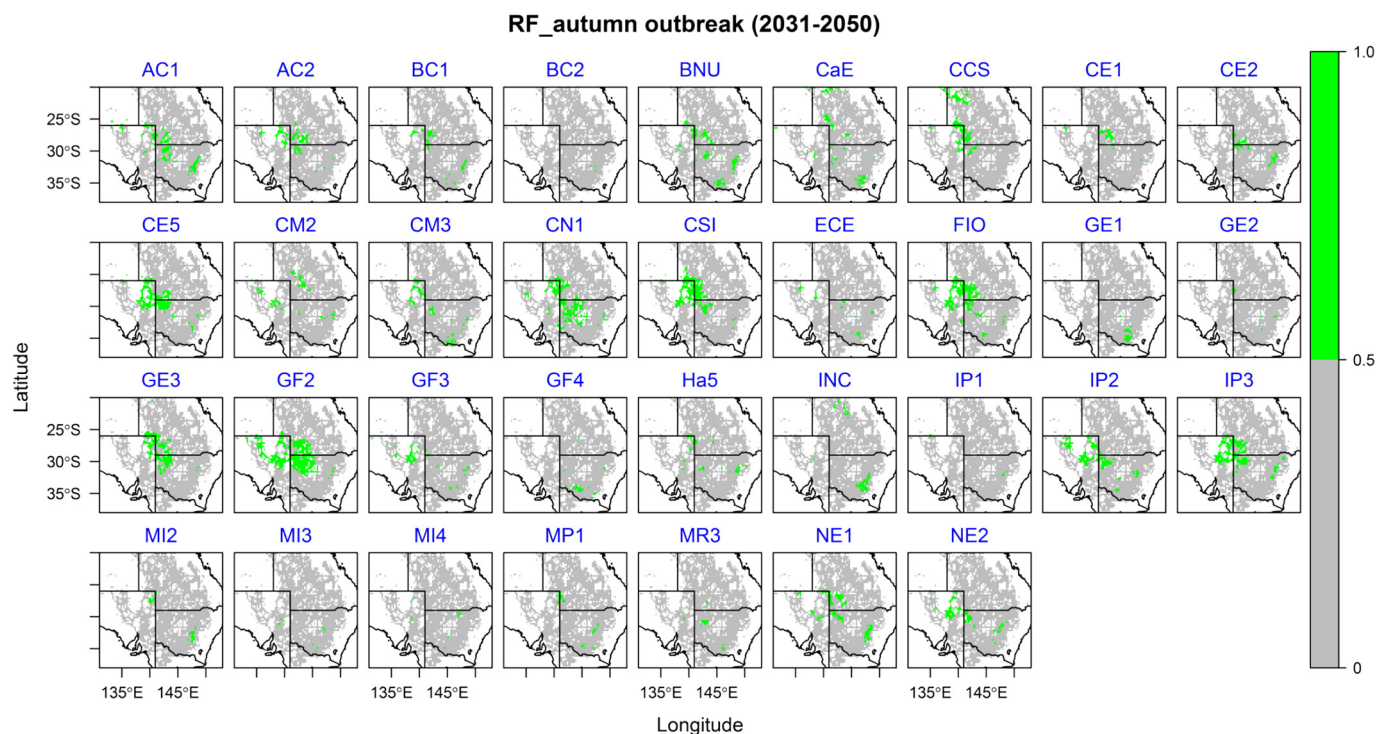


Fig. 6. The spatial distribution of the probability of Australian plague locust outbreaks in autumn during 2031–2050 projected by random forest (RF) model based on climate projections from 34 GCMs under RCP8.5.

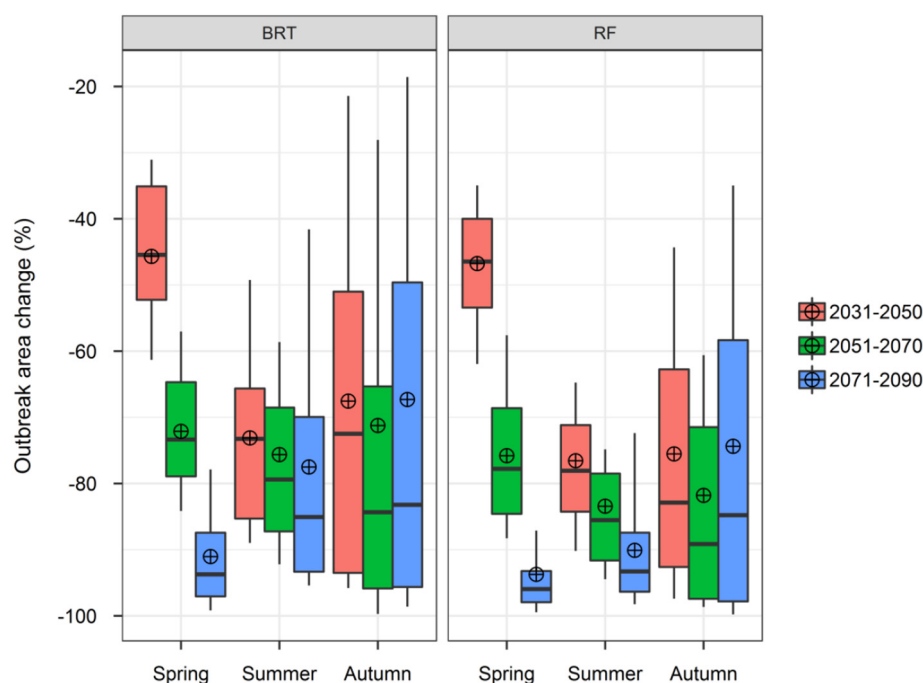


Fig. 7. Projected changes in the area of climatic suitability for Australian plague locust outbreaks in spring, summer and autumn during 2031–2050, 2051–2070 and 2071–2090 under the RCP8.5 scenario based on random forest (RF) and boosted regression tree (BRT) models. Box boundaries indicate the 25th and 75th percentiles across 34 GCMs, whiskers below and above the box indicate the 10th and 90th percentiles. The black lines and crosshairs within each box indicate the multi-model median and mean, respectively.

used for each season were derived from monthly temperature and rainfall values, which mainly capture annual variation and seasonal conditions. Compared to monthly temperature and rainfall averages, they are more biologically and ecologically meaningful (Guo et al., 2017). We developed RF and BT models of seasonal outbreaks as functions of different suites of climate variables for different seasons. In our study, the RF model and BRT models appeared to be reasonably accurate when validated against withheld outbreak/non-outbreak data. They showed a similar performance in predicting APL outbreaks regardless of season, though the predictive accuracy of SDMs was higher in spring with mean AUC of 0.94 than that in summer and autumn with mean AUC of 0.80. The Kappa statistic for summer and autumn outbreaks, however, indicate more marginal performance (~0.4 for the RF model). This is likely due to the broad distribution of autumn and summer outbreaks across several climatic regions (Fig. S2) and sparse climate sites scattered at the border of QLD, SA and NSW (Wang et al., 2018a). Although the modelling accuracy also depends on the factors like spatial resolution, size of the study area, methods and quality of input datasets (Chitale et al., 2014), our study overall shows an acceptable model performance based on these two statistics.

For each model, we demonstrated the partial effect of the two most important variables on the spatial distribution of APL outbreaks, having first ranked the relative importance of each of the significant variables. Precipitation seasonality followed by mean temperature of coldest quarter (winter) made the largest contributions to the spatial distribution of outbreaks in spring. Both spring models indicated that the probability of outbreaks is influenced by low precipitation seasonality. This

result may be explained by the fact that spring outbreaks occur over much of the area of uniform seasonal rainfall, mostly in NSW. The optimal mean temperature of the coldest quarter is less than approximately 12 °C. Cold climate is associated with the winter-dominated rainfall zone and therefore high soil moisture levels. Although nymphs are generally not present in June–August, our results support field observation that wet soil condition during winter is a critical prerequisite for egg development in early spring (Wright, 1987).

In contrast, we found that summer outbreaks are mainly influenced by temperature variables, namely mean temperature of driest quarter and mean diurnal range. Overall, the spatial distribution of observed outbreaks in summer is widespread across the study area (Fig. S2). The northern part of eastern Australia is subject to strong tropical influences with low mean diurnal temperature range and predominately summer rainfall, whereas the southern part has a large mean diurnal range and winter-dominant rainfall. This is the reason why there are two optimal intervals for mean diurnal range (approximately 12.5–13.2 °C and 15.5–16.2 °C) that are suitable for APL outbreaks in summer (Fig. 3b). The driest quarter, namely summer in the south and winter in the north had optimal mean temperature ranges of 20–22 and 11–12 °C, respectively. With respect to autumn outbreaks, high rainfall in the driest quarter and high temperature seasonality facilitates outbreaks (Fig. 3c). This could be due to many autumn outbreak records being distributed in inland areas (i.e. western parts of the study area) (Fig. S2) where rainfall is the main constraint for APL development and temperature has a large seasonality (Wright, 1987), but autumn records are limited for southern SA and VIC.

Table 1
Regression coefficients of changes in the area (percentage) of Australian plague locust outbreak predicted by random forest (RF) model in spring, summer and autumn with changes of bioclimatic variables selected by stepwise regression using AIC value.

	Δbio1	Δbio2	Δbio4	Δbio10	Δbio11	Δbio12	Δbio14	Δbio15	Δbio16	Δbio18	R ²
Spring	–	–	–	–	–28.4**	–0.5**	3.1**	–1.1*	0.7**	–	0.98
Summer	–	–10.1	0.4**	–24.5**	–	–0.9**	6.0**	–2.7**	1.1	0.5	0.93
Autumn	76.8*	–	1.8**	–97.0**	–	–1.1**	8.4*	–2.7*	1.8*	–	0.82

* $p < 0.05$.

** $p < 0.01$.

Table 2

Regression coefficients of changes in the area (percentage) of Australian plague locust outbreak predicted by boosted regression tree (BRT) model in spring, summer and autumn with changes of bioclimatic variables selected by stepwise regression using AIC value.

	Δbio1	Δbio2	Δbio4	Δbio5	Δbio10	Δbio11	Δbio12	Δbio14	Δbio15	Δbio16	Δbio17	R ²
Spring	–	–6.4*	–	–	–	–27.7**	–0.5**	2.6**	–1.2**	0.7**	–	0.98
Summer	43.8	–24.9*	1.0**	14.1	–78.5*	–	–0.6*	11.1**	–3.0**	1.3*	–2.0	0.91
Autumn	–	–	1.5**	–	–19.0**	–	–0.9**	6.9*	–2.6	1.9*	–	0.78

* $p < 0.05$.

** $p < 0.01$.

4.2. Future conditions for APL outbreaks

Several studies predict that global warming will alter areas of suitable bioclimatic conditions and shift climate suitability toward the high-latitude areas for a range of invertebrate species (Macfadyen et al., 2018; Ramirez-Cabral et al., 2018). These results are consistent with the outputs of our SDMs under modelled future climate, that show a contraction of areas with a greater than even chance of APL outbreaks occurring to cooler regions of study area, especially for the spring season. However, the area of probable outbreaks will be significantly reduced in all seasons by the end of this century. An obvious explanation for these results is the projected increase in periods of higher temperatures and reduced rainfall in eastern Australia at the end of this century, relative to current climate (CSIRO and BoM, 2015). Examination of regression coefficients of each of climate variable's contribution to the decrease in area of summer and autumn outbreaks (Tables 1 & 2) demonstrate how ΔBio 10 (mean temperature of warmest quarter) and ΔBio 14 (precipitation in the driest month) were both highly significant. In line with projected decreases in rainfall during spring and winter in the late decades of this century (CSIRO and BoM, 2015), ΔBio16 (precipitation of wettest quarter) contributed significantly to the reduction in the area of probable spring outbreak events.

Global climate models are a standard tool to derive projections for future climate change. The consensus is that SDMs calibrated by historical data and driven by multiple GCM outputs, provide the best way for predicting future changes to species distribution under climate change (Hof et al., 2018). Previous research investigating the impacts of future climate projections have generally selected only a few GCMs at most (Briscoe et al., 2016; Macfadyen et al., 2018; Radinger et al., 2017). However, choosing only a few GCMs may lead to potentially biased results or results that are not particularly useful for assessing uncertainty in future climate impacts because the sample size is too small. Our work is based on the climate projections from 34 GCMs outputs, which we used to drive SDMs to produce an ensemble of projected changes in probable seasonal outbreak areas (Fig. 7). Although our models suggest that the overall area of likely locust outbreaks will be reduced, there is considerable regional variation. Areas located in north-western NSW and south-western QLD still have a high probability of APL outbreak, especially in autumn under climate change for these models like CE5, CN1, CSI, FIO, GE3, GF2, IP2 and IP3 (Fig. 6).

The use of climate-based SDMs to explore range shifts of different species is an active research area, and the different ways in which climate variables are accounted for and analysed vary enormously between studies owing to the particular questions being investigated and study-specific assumptions (Fordham et al., 2017; Peterson et al., 2018). Although we used a climate-based SDM for our work, we restricted our analyses of APL outbreaks to the current APL habitat, and did not study whether the expansion of climatic suitability for APL outbreaks will shift further southwards (high latitudes). While some regions in southern Victoria may become climatically more suitable for spring outbreaks, they occur in forested areas which are not preferred by locusts. However, it is possible that forest areas turn to grasslands in the future due to climate change and land degradation to some extent. Thus not only the climate, but also the vegetation types are suitable for locusts in those areas. Future work using the complexity and power of process-based models of vegetation dynamics as a function of

climate, land-use and disturbances (Rabin et al. 2017; Haverd et al. 2018) may be able to assess how future climate could result in changes to the extent of grasslands preferred by locusts at the expense of forests in south-eastern Australia. From an operational point of view, our results may be useful for locust surveillance and control operations by better targeting the areas to be monitored. Previous work has demonstrated the usefulness of SDMs in reducing the high costs of survey and control campaigns (Lazar et al., 2016). Our modelling results imply that climate-based forecasts of APL are possible and APL management under climate change needs to take into account significant potential shifts in APL distribution in future decades.

4.3. The implication of this study on APL management

The principal anthropospheric interactions with locusts are agricultural land use and locust control operations. Land use practices and policy are likely to play a major role in the distribution and condition of locust habitats in the future. Locust control activities produce transient local altered species abundances, affecting a very small proportion of the distribution area. Outbreak data include all control activities because control occurs in response to existing outbreaks. While it is possible that control activities could have reduced the abundance of subsequent generations, changes through time were not analysed in this study.

The results of our modelling suggest that the overall area of likely locust outbreaks will be reduced. However, this does not necessarily imply a reduced need for management intervention in future decades given the uncertainties over the climate projections, the biodiversity, ecosystem functioning and agricultural consequences of climate change in APL habitats. The extent of future grazing land or cropland in Australia will be influenced by a complex array of non-biophysical factors such as land-use practices, environmental and trade policy, which play an important role in the distribution and condition of locust habitats. And our study only focused on utilising the readily available rainfall and temperature data from the CMIP5 archive, and applying our SDMs into the future based on those data. More-specialised studies of the CMIP5 and related GCM databases, report that as a result of future increase in greenhouse warming, inter-annual variability in ENSO and the Indian Ocean Dipole (IOD)- two of the main synoptic drivers of rainfall and temperature across much of eastern Australia will also increase (Cai et al., 2018a; Cai et al., 2018b). In addition, CMIP5 studies indicate that future winters across eastern Australia will become milder (CSIRO and BoM, 2015), which could alter autumn-winter population dynamics. The complex uncertain nature of these bio-physical and non-biophysical drivers, indicate that additional research is needed to disentangle their potential impacts on future APL populations.

4.4. Study limitations and uncertainty

We ran each SDM 100 times and used a weighted ensemble approach to predictive performance to increase model reliability. Our two SDMs for each season had similar predictive ability as measured by AUC under the current climate, but the spatial distribution of outbreak probability under future climate still presented differences for some GCMs between BRT and RF especially in autumn. This discrepancy may be associated with the difference between algorithm structures

when projected to new environmental conditions (temperature increase and rainfall patterns change).

The prediction of seasonal outbreaks in summer and autumn were less performant in terms of AUC and Kappa indices due to the spatial segregation of the areas of outbreaks. This could decrease the confidence in predicting the outbreaks areas under future climate change scenarios. Our bioclimatic SDM approach did not account for APL life history traits and population biology or their interaction in changing climate. Temperature controls the rates of locust development so higher mean temperature will change the timing of spring emergence. Although breeding cycles are initiated and limited by rainfall events, an extra generation is potentially possible in some regions. The possibility of changes to population sequences and migration exchanges under altered climatic conditions were also not considered here.

Many non-climatic factors also affect locust distribution, such as woody plant cover, grass productivity, soil physical properties, soil moisture and topography. Previous work has attempted to include non-climatic variables such as land cover and vegetation types in empirically-based models of locust population dynamics (Piou et al., 2013; Veran et al., 2015). Improvements in the prediction of the spatial distribution of locust outbreaks are theoretically possible by integrating non-climatic variables and considering migration processes. However, the way forward regarding which, if any, currently available modelling framework to use (of which SDMs is one of many options) remains an open question due to the range of complex and non-linear interactions between climate and non-climate variables plus demographic processes.

In addition, recent research has shown that accounting for extreme events in SDMs is also important, especially considering the increased likelihood of droughts and heatwaves under climate change (Morán-Ordóñez et al., 2018; Overgaard et al., 2014). APL is an arid zone insect, but periods of extreme high temperature ($>47^{\circ}\text{C}$) are likely to affect its survival and population persistence, particularly in newly hatched nymphs (Woodman, 2011). The effects of changed climate and extreme events on locust habitats has received little research attention to date, although considerable work by the terrestrial carbon research community has addressed the impact of climate change and variability on relevant landscapes e.g. rangelands through modelling and remotely sensed data (Boone et al., 2017; Wang et al., 2018b).

There are methodological sources of uncertainty in our study which may influence the results we generated here. SDMs are useful tools for investigating likely geographic range changes of species under different climatic domains. In our case, we applied SDMs to the occurrence of high density nymph populations rather than all species occurrence records. SDMs built from bioclimatic variables, without incorporating phenology, population biology or specific physiological constraints, may be more appropriate to sessile organisms or those with limited dispersal capacities, than to widespread migratory insects like locusts. Previous studies have suggested using multiple SDMs ensemble approaches to reduce the uncertainty arising from particular SDM algorithms, which may propagate potential biases in the predicted suitable habitat for a species (Garcia et al., 2012). In this study we used multi-model weighted ensemble means to reduce the uncertainty caused by single SDMs (Keenan et al., 2011; Wang et al., 2018a). For our assessment of locust outbreaks under future climate change we only accounted for the GCM outputs driven by the most extreme radiative forcing scenario, RCP8.5, and those generated from other relatively more moderate radiative forcings e.g. RCPs 2.6, 4.5, 6.0 were not considered. Therefore, the uncertainty due to scenarios especially for rainfall in the future (distribution, seasonality and quantity) was not taken into account in this study.

5. Conclusions

This study analysed relationships between a range of bioclimatic variables and the occurrence of APL outbreaks using SDMs, and then

assessed the potential impacts of climate change on the future probability of APL outbreaks. The RF and BRT algorithms were used to construct the SDMs provide information on the individual contribution of each bioclimatic variable on the spatial distribution of the probability of APL outbreaks. Our use of climate outputs from 34 available GCMs increases the robustness of our findings because this large GCM ensemble covers the widest range of possible future climate change projections based on the best available climate science. Our modelling predicts that areas of climatic suitability for APL outbreaks in spring will decrease dramatically in eastern Australia, contracting to small areas in the southern species range by the 2080s. Similar decreasing trends will occur in summer and autumn, but the results are not as clear cut compared with spring. In addition, there will be regional variation in the probability of APL outbreaks for each season due to variability in projected climates. Our novel study can help inform adaptive management policies for outbreaks of APL and other pest species under future climate change in Australia.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.02.439>.

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